DISTRIBUTION OF FOUR SPECIES OF *NEPHTYS* (POLYCHAETA) IN THE ESTUARINE AREA OF THE RIVERS RHINE, MEUSE, AND SCHELDT

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Extrait de « Vie et Milieu »

Troisième Symposium Européen de Biologie Marine

Supplément n° 22 — 1971 — pages 677-699

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Quatre espèces de *Nephtys* se trouvent dans la région estuarienne des fleuves Rhin, Meuse et Escaut dans la partie sud-ouest des Pays-Bas et dans la région adjacente de la Mer du Nord. Il s'agit de *N. caeca, N. cirrosa, N. hombergii* et *N. longosetosa.*

N. cirrosa fut absente durant trois ans, après l'hiver rigoureux de 1962-1963.

Toutes les espèces paraissent avoir la même tolérance envers les salinités inférieures; leur limite inférieure paraît être d'environ 12 ‰ Cl.

Les espèces se trouvent très souvent ensemble, mais, néanmoins, il est possible de les séparer en un groupe se composant de *N. caeca* et *N. hombergii,* vivant dans les sables fins et vaseux, et un autre groupe se composant de *N. cirrosa* et *N. longosetosa,* vivant dans les sables grossiers et non vaseux.

Il y a de petites différences écologiques, en particulier relativement à la distribution verticale, entre *N. caeca* et *N. hombergii.* Il n'est pas possible de démontrer des différences écologiques entre *N. cirrosa* et *N. longosetosa.*

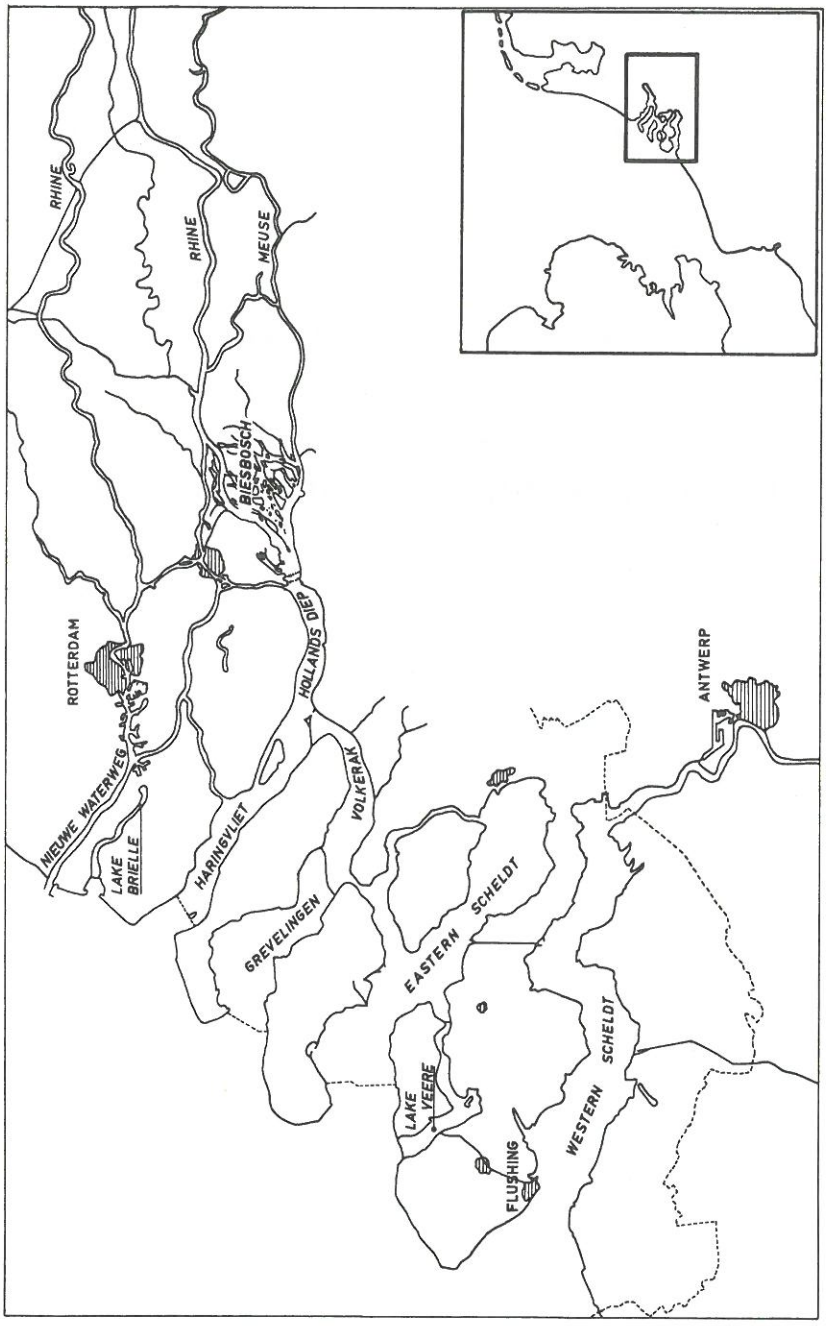

FIG. 1. — Map of the Delta area.

Introduction

It is generally accepted in ecology that two or more species with similar ecological requirements cannot fill the same niche in one and the same biocenosis. This hypothesis is known as Gause's principle or as the competitive exclusion principle (Hardin, 1960).

All the European species of the genus *Nephtys* have a very similar morphology; moreover probably all species are free-living predators in soft sediments. Although Fauchald (1963) was able to demonstrate different depth-ranges for some species, a group of four species inhabits the shallow coastal waters of the southern part of the North Sea and the adjacent areas. Grab-samples often contain two or three species and on a few occasions I have even found all of them in one such sample. It therefore seemed interesting to investigate the validity of Gause's principle in these species.

This group of species, consisting of *Nephtys caeca* (Fabricius, 1780), *Nephtys cirrosa* Ehlers 1868, *Nephtys hombergii* Savigny 1818, and *Nephtys longosetosa* Oersted 1842, has been found in SW England and Wales (Clark & Haderlie, 1960), around the Isle of Man (Southward, 1956), in Loch Ewe in Scotland (McIntyre & Eleftheriou, 1968), Yorkshire (Jones, 1955), Norfolk (Hamond, 1966), Essex (Davis, 1967), Roscoff in Brittany (Rullier, 1959), the German Bight (Friedrich, 1938; Westheide, 1966), and in the Delta area in The Netherlands (own observations). It was in the last of these areas that we tried to determine whether competitive exclusion exists among these species.

Description of the area investigated

The Delta area covers the estuarine region of the rivers Rhine, Meuse, and Scheldt in the southwestern part of The Netherlands. The hydrography of the area (fig. 1) was described by Den Hartog (1963) and Peelen (1967), from whose publications the salinity data in this paper are quoted. The estuaries in this area are all of the gradient type.

In the tidal channels and in the intertidal zone of the estuaries, muddy sands predominate together with cleaner sands having median grain-sizes ranging from 100 μ to 300 μ. In the adjacent part of the North Sea, however, only fairly clean sands occur, mostly with median grain-sizes between 200 μ and 500 μ. Muddy areas are rare.

The depth of the tidal channels is maximally about 50 m, but generally varies between 10 and 20 m. The adjacent part of the North Sea is in general 15 to 35 m deep.

The tidal difference in the investigated area varies between 2 and 5 m.

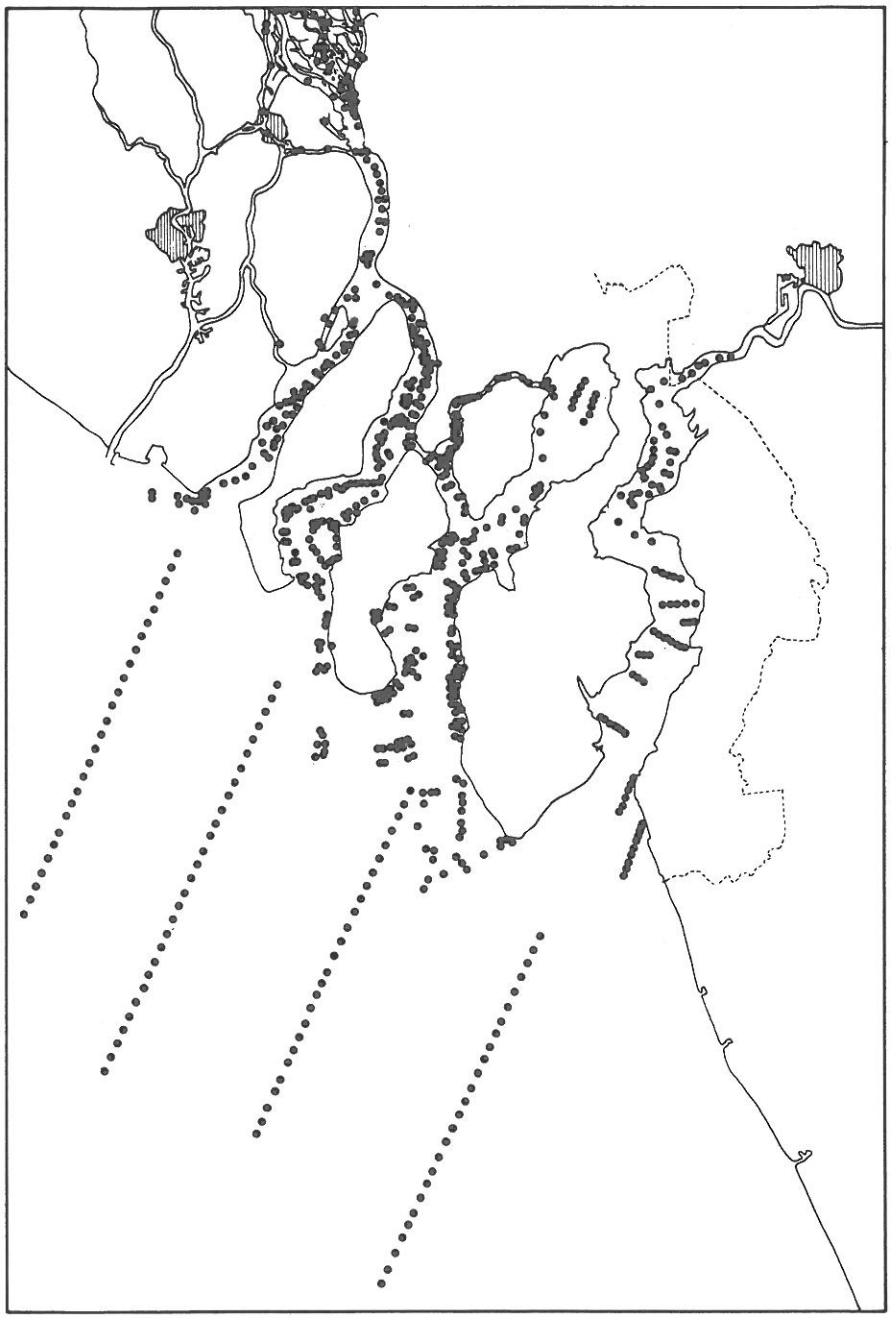

FIG. 2. — Location of all grab-samples taken between 1961 and 1967.

Methods

The majority of the subtidal samples were obtained with a 0.1 m^2 Van Veen grab, but the samples from the North Sea were taken with a 0.2 m^2 grab of the same type. These samples were sieved aboard through a 1 mm sieve, preserved in 4 % neutralized formalin and sorted by hand in the laboratory. Intertidal samples were treated similarly, but were obtained by digging out sampling quadrats during low tide.

Fig. 2 shows the positions of all grab-samples; the intertidal sampling stations are omitted, because the results they supplied were barely used in this study. Owing to technical difficulties the sampling had to be extended over seven years (1961-1967).

All depths recorded are calculated below mean low-water-level.

The sediment data was obtained by means of a series of graded sieves with mesh-widths of : 1 000, 600, 420, 300, 210, 150, and 105 μ. From this data, the median grain-size and a sorting-coefficient were calculated with the methods described by Inman (1952).

To test the significance of observed distributional differences between two species, a χ^2 test was applied.

Geographical distribution

Nephtys hombergii seems to be a cosmopolitic species (Fauchald, l.c.); it is certainly common all along the Atlantic shores of Europe.

N. caeca is a common species in northern Europe (Fauvel, 1923; Fauchald, l.c.); its southernmost localities are on the Atlantic coasts of France. Hence, a very large part of its area is shared with *N. hombergii.*

N. longosetosa is an arctic species, reaching its southern limit in the Channel area (Fauchald, l.c.; Clark & Haderlie, l.c.). It, too, has a large part of its area in common with *N. hombergii* and also with *N. caeca.*

N. cirrosa, on the contrary, is a southern species, its northern limits lying in Scotland (McIntyre & Eleftheriou, l.c.) and the German Bight of the North Sea where it is recorded from Ostfriesland by Friedrich (l.c.). Evidently, the areas of *N. cirrosa* and *N. longosetosa* only overlap to a small extent. It shares an important part of its area with *N. caeca* and *N. hombergii,* however.

The southern origin of *N. cirrosa* was also demonstrated by the effects of the very severe winter of 1962/1963, when water temperatures in the Delta area fell well below 0 °C (Boddeke, 1963). In the preceding summer all of the four species in question had been abundant in the Delta area, but none of the 400 samples taken in the summer of 1963 showed a single specimen of *N. cirrosa,* and the species remained absent until 1966.

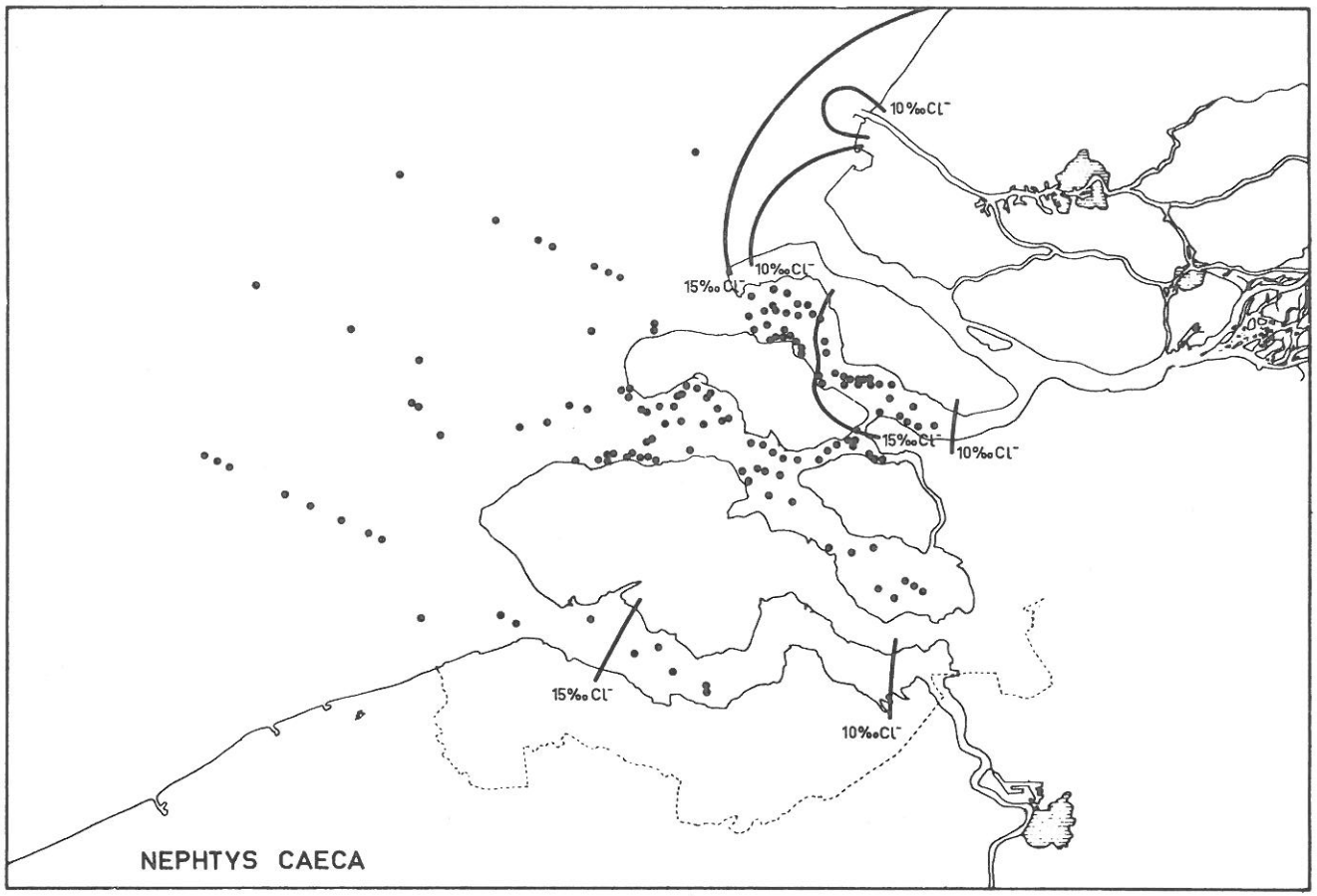

FIG. 3. — Distribution of *Nephtys caeca*. Only grab-sample data are incorporated. Isohalines represent mid-tide conditions during average river discharge.

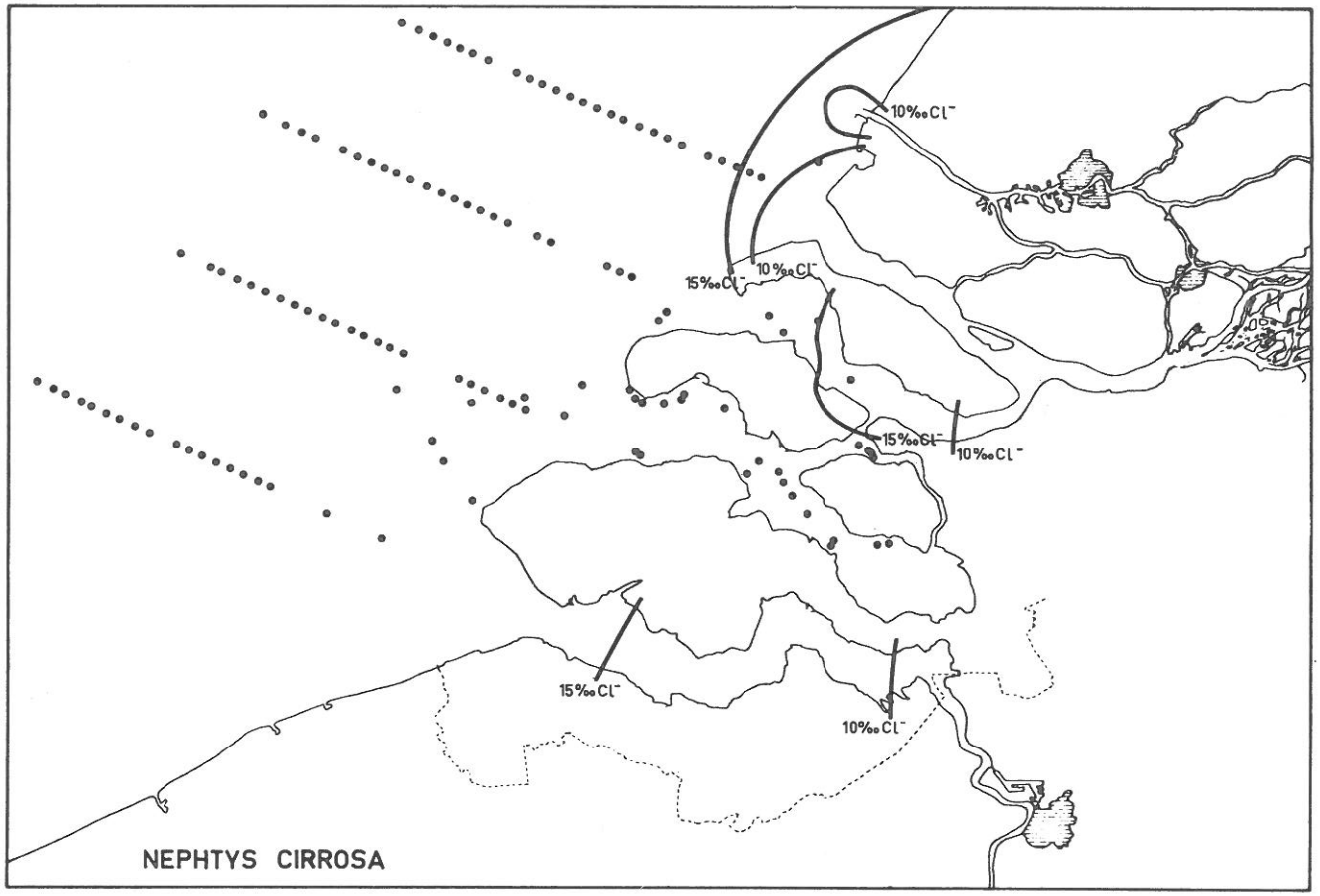

FIG. 4. — Distribution of *Nephtys cirrosa*. Only grab-sample data are incorporated. Isohalines represent mid-tide conditions during average river discharge.

Influence of salinity

Figs. 3-6 show all the grab-sample data of the four species, as well as the surface isohalines of 10 and 15 °/₀₀ Cl' at half tide during average river discharge. However, not too much importance should be assigned to these isohalines for four reasons. Firstly, these isohalines move to and fro under the influence of the tides, and secondly, their position also changes under the influence of the varying amount of river discharge. In the third place, we were only able to draw surface isohalines, but in the estuaries concerned the bottom isohalines are shifted to some degree in an upward direction. Lastly, it should be noted that the animals probably are influenced much more by the interstitial water than the overlying water masses, because they do not possess a permanent tube to the surface of the sediment. Although Jones (l.c.) states that the animals irrigate their impermanent burrow when covered by water, we suppose that they withdraw during periods of low salinity. Arguments have been put forward for the supposition (Reid, 1932; Smith, 1956; Sanders, Mangelsdorf & Hampson, 1965; Johnson, 1967), that the salinity of the interstitial water often is fairly stable and roughly represents the average conditions in the overlying waters. Therefore, the isohalines mentioned above may nevertheless be a good indication of the interstitial salinity conditions in the same area.

The data obtained in the Western Scheldt suggest that *N. caeca, N. hombergii,* and *N. longosetosa* have about the same tolerance for lowered salinities. Their lower limit certainly lies above 10 °/₀₀ Cl' and is probably slightly under 15 °/₀₀ Cl'. It may be estimated to be about 13 °/₀₀ Cl', as in a preliminary experiment specimens of *N. hombergii* died in water of a salinity of 12 °/₀₀, whereas other specimens remained alive in 13.86 °/₀₀ Cl'. In the with regard to salinity much more complicated Volkerak area, where *N. longosetosa* is absent, probably because a suitable substrate is lacking (see p. 692), this value seems to be confirmed for *N. caeca* and *N. hombergii.* Since the sampling in these areas was carried out during the period in which *N. cirrosa* was absent due to the effects of the cold winter of 1962/1963, nothing can be inferred about the salinity tolerance of this species, but the 1961 observations in the Haringvliet area point to a similar salinity tolerance in this species.

Therefore, I conclude that niche diversification among these four shallow water species of *Nephtys* is not achieved by divergent tolerance for low salinities.

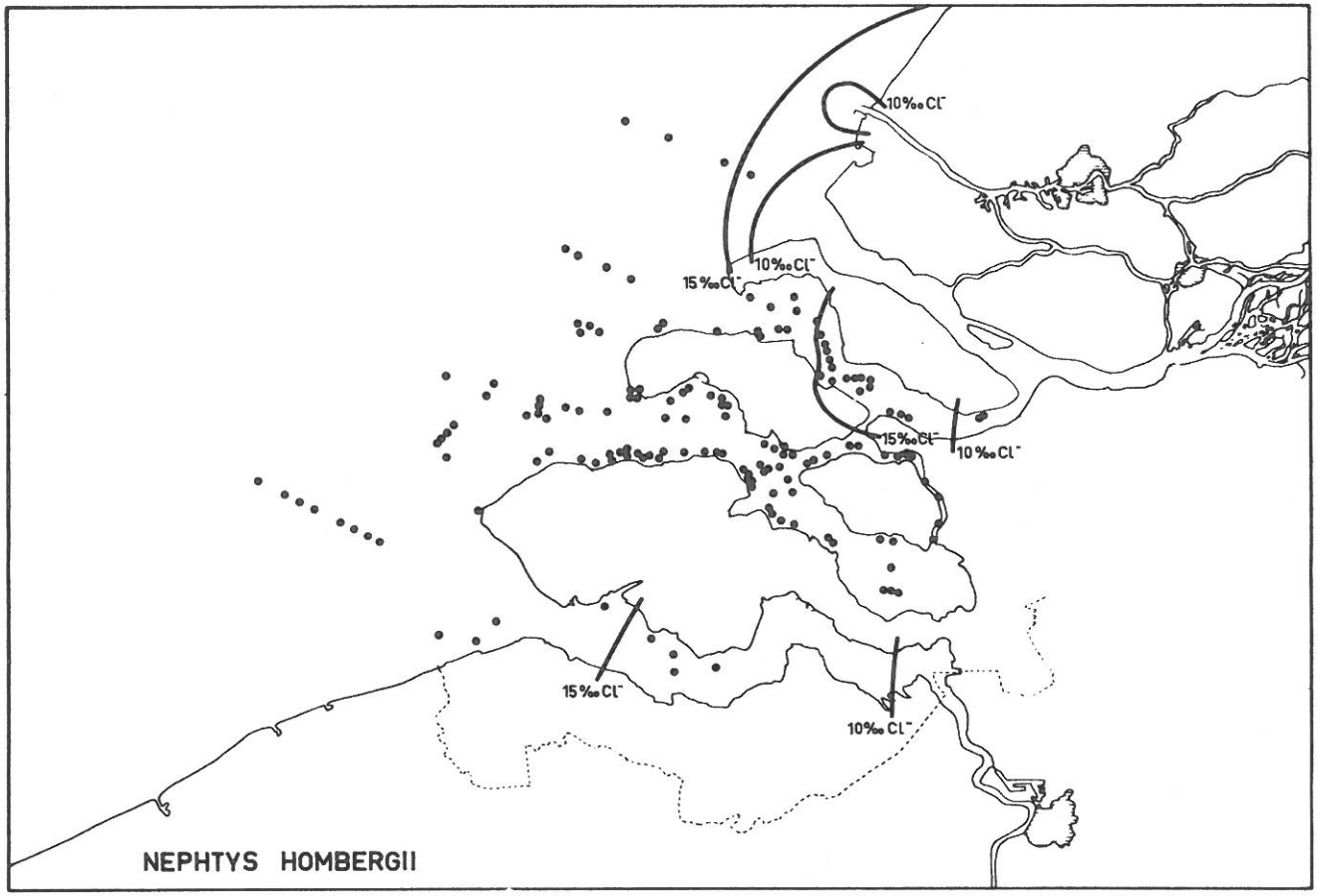

FIG. 5. — Distribution of *Nephtys hombergii*. Only grab-sample data are incorporated. Isohalines represent mid-tide conditions during average river discharge.

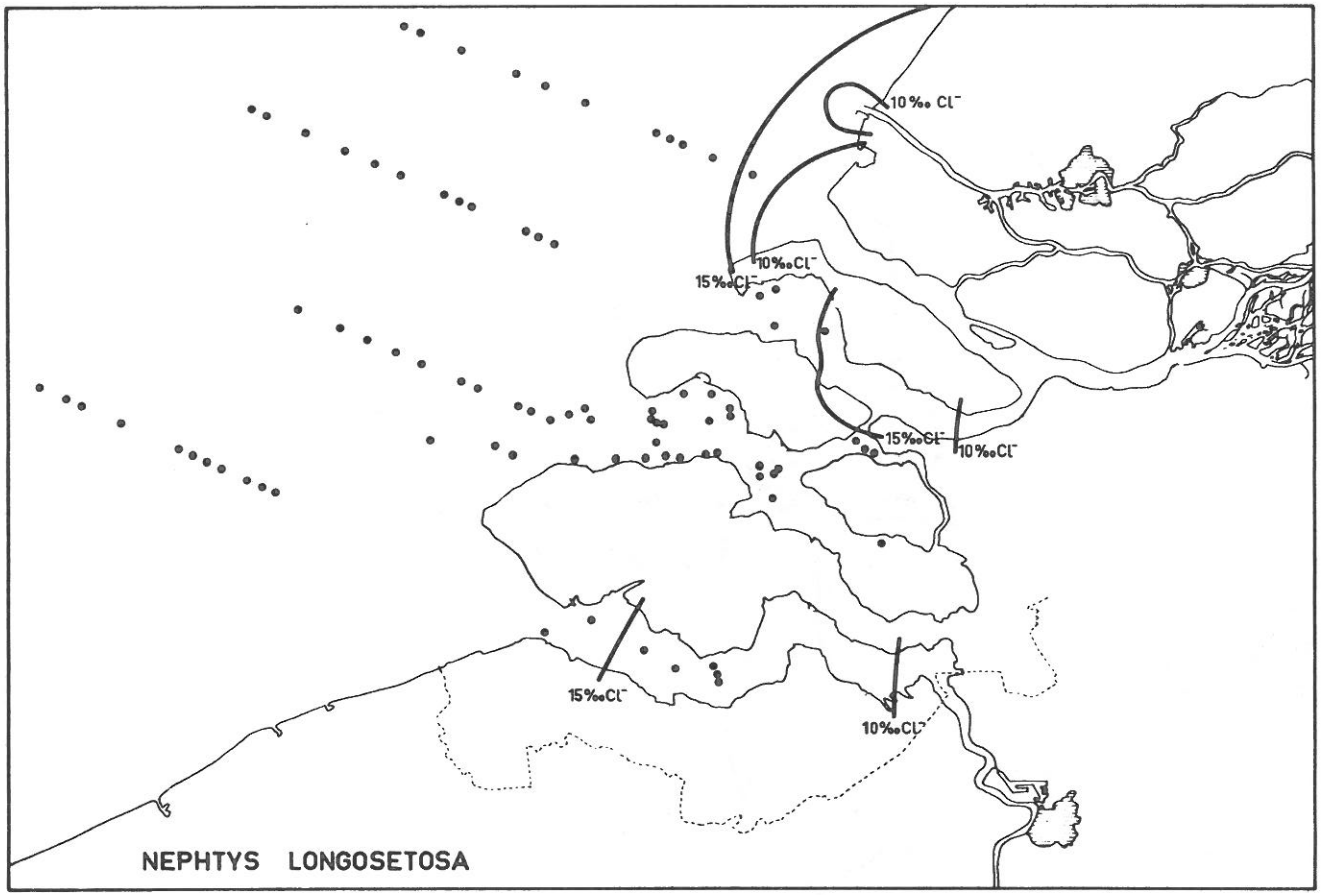

FIG. 6. — Distribution of *Nephtys longosetosa*. Only grab-sample data are incorporated. Isohalines represent mid-tide conditions during average river discharge.

Vertical distribution

In clean sandy beaches *N. cirrosa* may occur in large numbers, as was shown by Clark & Haderlie (l.c.), McIntyre & Eleftheriou (l.c.) and our own results. We also found *N. longosetosa* abundantly in very similar sandflats kept clean by tidal scour. Thus, both species may occur intertidally. The subtidal vertical distribution of these species is also very similar, as is shown by fig. 7. Statistically, there is no significant difference between the subtidal depth distribution of these two species ($0.25 > P > 0.10$).

Our data, however, show a very significant difference with respect to depth between *N. longosetosa* and *N. caeca,* and also *N. hombergii. N. longosetosa* occurs deeper than *N. caeca* ($P < 0.0005$) and also deeper than *N. hombergii* ($P < 0.0005$). For *N. cirrosa* this test could not be applied owing to lack of suitable data, but on the basis of its similarity to *N. longosetosa,* it too may be assumed to occur deeper than *N. caeca* and *N. hombergii.*

N. hombergii is abundant in the muddy sandflats emerging along the estuaries during falling tide. *N. caeca,* on the other hand, was found only once in the intertidal zone. Subtidally, *N. caeca* seems to inhabit relativily deeper areas than *N. hombergii* (fig. 7), but this difference is not significant ($0.25 > P > 0.10$).

Thus, *N. cirrosa* and *N. longosetosa,* which do not show differences in their depth distribution, occur subtidally in the deeper part of the tidal channels, whereas *N. caeca* and *N. hombergii,* which also do not show differences in their subtidal depth distribution, inhabit the shallower parts. *N. caeca,* however, is absent from the intertidal zone, where *N. hombergii* is abundant.

Influence of substrate

Clark & Haderlie (l.c.) have reported that *N. cirrosa* and *N. hombergii* inhabit different types of sediment in the beaches of SW England and Wales : the former lives in clean sandy beaches, the latter in more or less muddy sands. Nevertheless, there appeared to be several beaches with both species living together.

These findings prompted us to make a more detailed study of the nature of the sediment. Fig. 8 shows the grab-samples classified according to their median grain-size, and within each class the number of samples containing the species of *Nephtys* concerned is indicated.

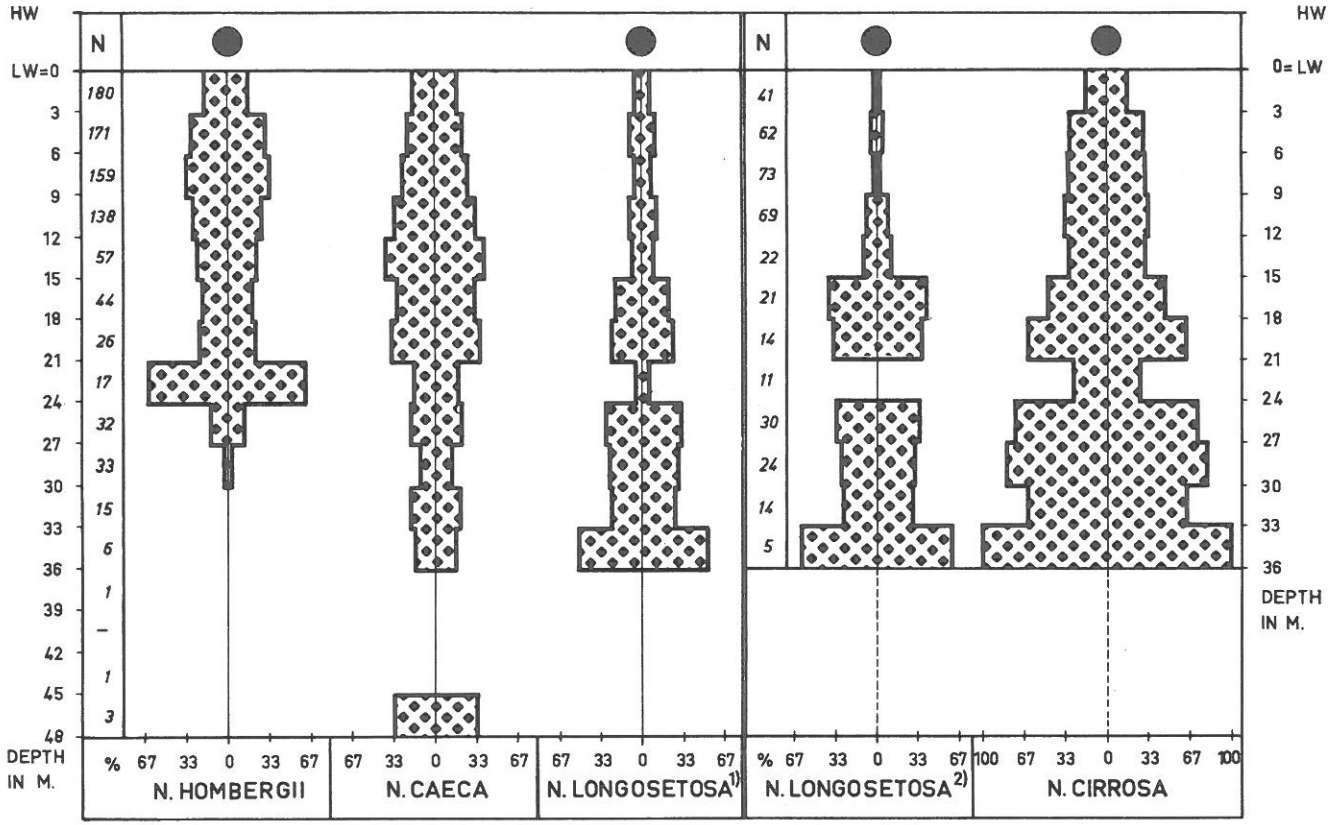

FIG. 7. — Vertical distribution of *Nephtys caeca, N. cirrosa, N. hombergii,* and *N. longosetosa*. The large dots at the top indicate intertidal occurrence; the value at the bottom (horizontal axis) denote the percentage of the grab-samples in each depth-class containing the species in question. On the vertical axis the depth-classes (width 3 m) are represented, together with the number of grab-samples in each class. *N. longosetosa* first is compared with *N. hombergii* and *N. caeca* by means of the combined data of all sampling years (1); secondly this species is compared with *N. cirrosa* by means of the combined data of 1962 and 1966 (2), because the latter species was absent in the years in between.

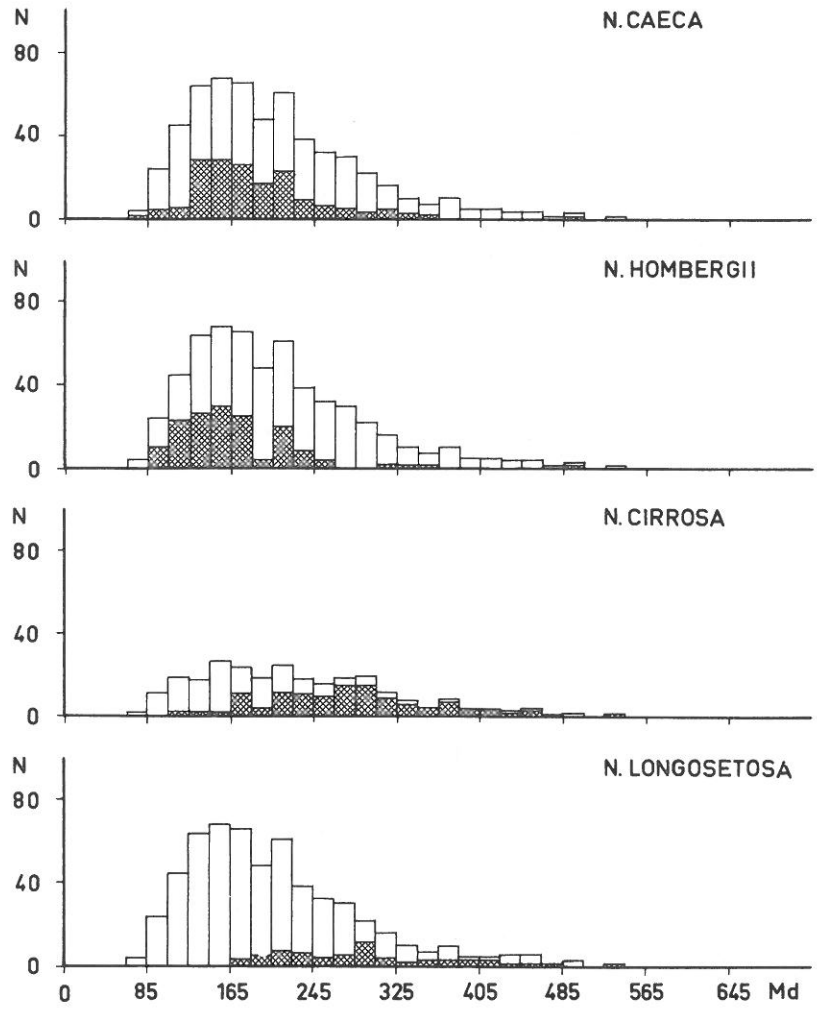

FIG. 8. — Median grain-size of the sediments inhabited by *Nephtys caeca*, *N. cirrosa*, *N. hombergii*, and *N. longosetosa*. The height of the column shows the total number of samples within a certain class of median grain-size; the hatched area shows the number of samples containing the species concerned.

From these results, two ecological groups of nephtyids can be clearly distinguished. One group, comprising *N. caeca* and *N. hombergii*, inhabits the more or less muddy sediments, whereas the other group, formed by *N. cirrosa* and *N. longosetosa*, lives in the more sandy substrates. This agrees very well with the results of

CLARK & HADERLIE (l.c.). It is interesting to see that similar ecological separations have been reported from other parts of the world, since CLARK & HADERLIE (l.c.) mention two other cases from American coasts.

Differences within these two ecological groups are less evident. *N. hombergii* seems to prefer sediments with a slightly higher mud content than those inhabited by *N. caeca*. The difference in the distribution of the median grain-sizes of the samples containing these species is indeed significant ($0.005 > P > 0.001$), but there is such a large overlap of their sediment ranges that I attempted to find further ecological differences between *N. caeca* and *N. hombergii*.

Not only the grain-size, but also the rate of sorting of a sediment determines the permeability of it (CALLAME, 1963). This factor governs the rate of water circulation and thus such environmental factors as the amount of available oxygen (BRAFIELD, 1964, 1965) and the temperature (JOHNSON, 1965) within the sediment. It was therefore of interest to determine wether the sediments inhabited by *N. caeca* showed sorting-coefficients different from those of the sediments inhabited by *N. hombergii*. The sediments inhabited by *N. caeca* do not seem to be sorted better or worse than those inhabited by *N. hombergii*, because no statistically significant difference between the distributions of the sorting-coefficients of the sediments inhabited by these species was found ($0.50 > P > 0.25$). This is also shown by figs. 9 and 11.

Since the grain-size distribution of a sediment is characterized to a great extent by its median grain-size and its sorting-coefficient and it was found that on the average *N. caeca* lives in slightly coarser sediments than *N. hombergii*, it is hardly surprising to find that on the average the $< 105\ \mu$ fraction is larger in sediments inhabited by *N. hombergii* than in those inhabited by *N. caeca*. No important differences were found for the $> 300\ \mu$ fraction.

Therefore, it must be concluded that there are minor differences between the sediments inhabited by *N. caeca* and those inhabited by *N. hombergii* with respect to the grain-size, but not with respect to the sorting-coefficient.

Fig. 8 suggests that *N. longosetosa* inhabits the same grades of sediment as does *N. cirrosa*. With the data available it is not possible to demonstrate a significant statistical difference between the distributions of the median grain-sizes of the sediments inhabited by these species ($0.75 > P > 0.50$).

From figs 10 and 12 it is obvious that there are also no important differences in the sorting-coefficients of the sediments inhabited by these species. The difference between these two distributions is indeed not statistically significant ($P \approx 0.075$).

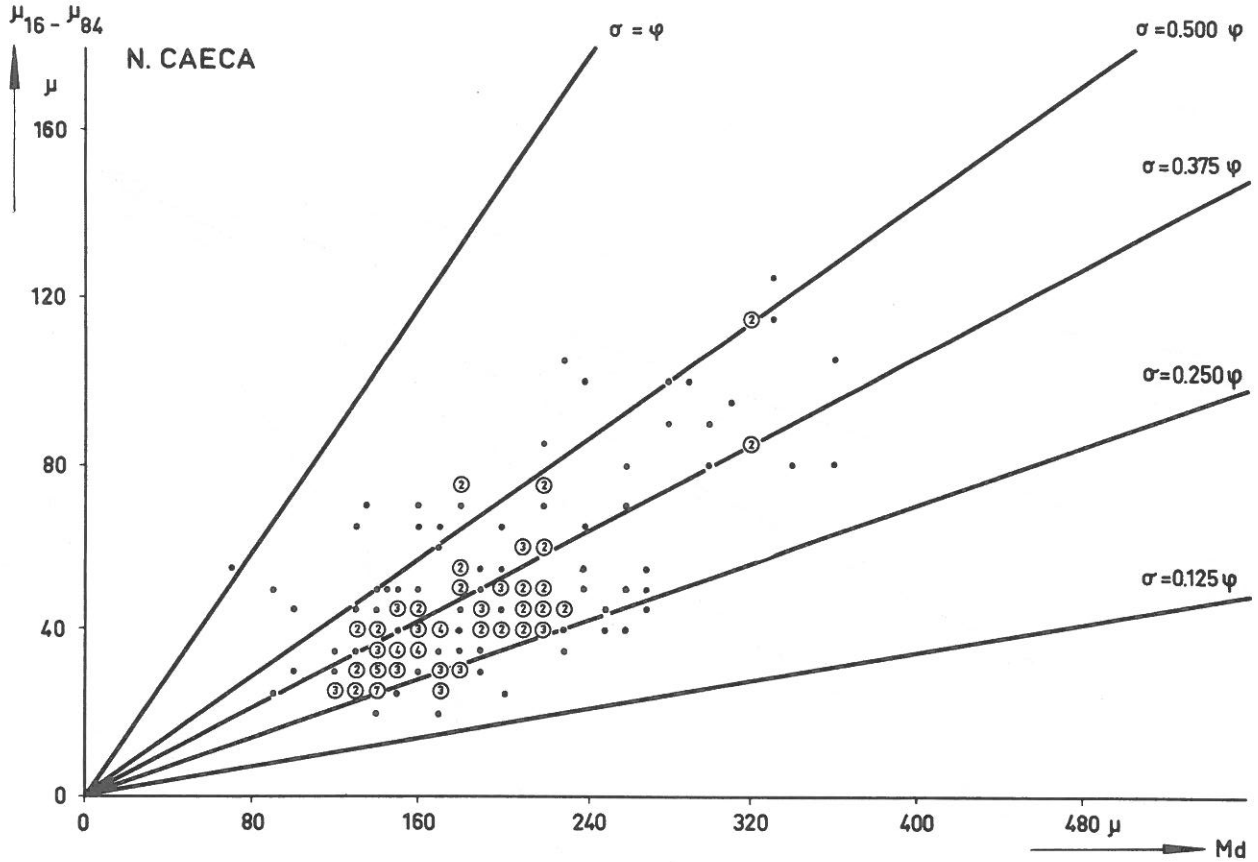

FIG. 9. — Rate of sorting of the sediments inhabited by *Nephtys caeca*. Horizontal axis : median grain-size of the samples; vertical axis : sorting-coefficient in μ. Some lines connecting points with the same sorting-coefficient, expressed in φ-units, have been drawn.

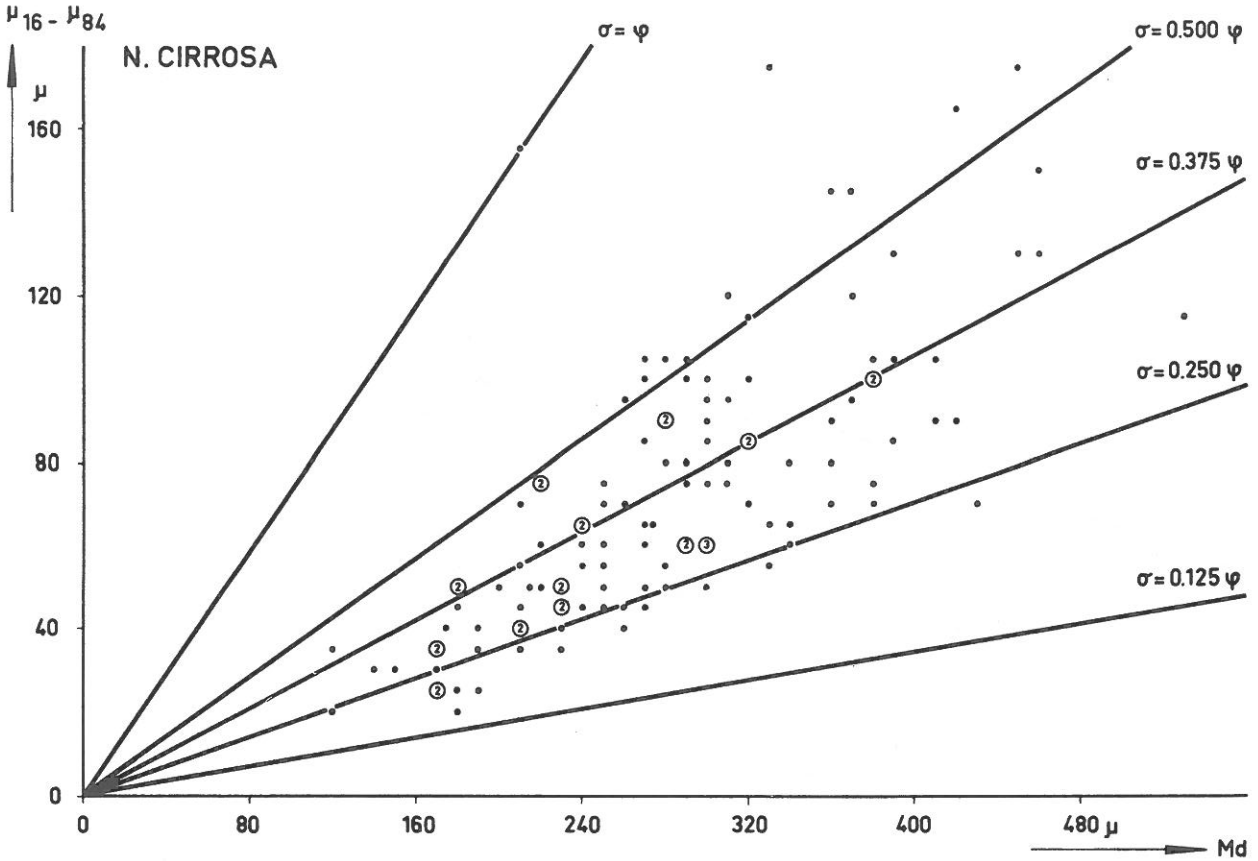

FIG. 10. — Rate of sorting of the sediments inhabited by *Nephtys cirrosa*. Horizontal axis : median grain-size of the samples; vertical axis : sorting-coefficient in μ. Some lines connecting points with the same sorting-coefficient, expressed in φ-units, have been drawn.

Thus, a certain niche diversification is present in the distribution over the various types of sediments. *N. hombergii* and *N. caeca* inhabit especially muddy sands, with the former species predominating in the finer grades. *N. cirrosa* and *N. longosetosa* live in clean sands, apparently without any difference in the type of substrate inhabited.

Discussion

The foregoing makes it clear that in the estuarine area of the rivers Rhine, Meuse, and Scheldt there are two ecological groups of nephtyids. The first group, consisting of *N. caeca* and *N. hombergii*, occurs in muddy sands and lives in the shallower part of the tidal channels. The other group, consisting of *N. cirrosa* and *N. longosetosa*, lives in clean sands and occurs especially in the deeper part of the gullies. Within the first group *N. hombergii* is usually found in slightly muddier sands than *N. caeca;* moreover, the former species unlike the latter, also occurs intertidally. Within the second group I have been unable to find any differences between the two species in question.

Although these differences seem to concern two factors, it must be pointed out that these factors are interdependent. It has been shown, for example by Postma (1957), that in tidal channels in an estuarine area the coarsest sediments are found in the deepest places, and that the coarseness decreases towards the edges of the gullies. My data from the Delta area wholly confirms these findings, and I therefore conclude that the differences in the distribution of nephtyids are caused by only one factor : either the nature of the sediment or the depth of the water.

For estuarine animals to the best of my knowledge, no correlation between depth distribution and pressure has ever been shown, and from what we know it does not seem very probable. For infauna species in an estuarine area, a correlation between vertical distribution and the depth of the water would most probably be dependent on an influence of temperature or of salinity. Since it has been shown that salinity does not cause distributional differences, it may be ruled out as a factor. Temperature does not seem very probable, because the species living deepest, and consequently in the most stable environment, also live intertidally, where the most extreme temperatures may be reached. Moreover, these species live in sandy sediments, and according to Johnson (1965), temperature conditions are most extreme in sandy sediments, so that higher temperatures are reached there than in muddy substrates. It is therefore justified to conclude that the subtidal distribution of the four species of

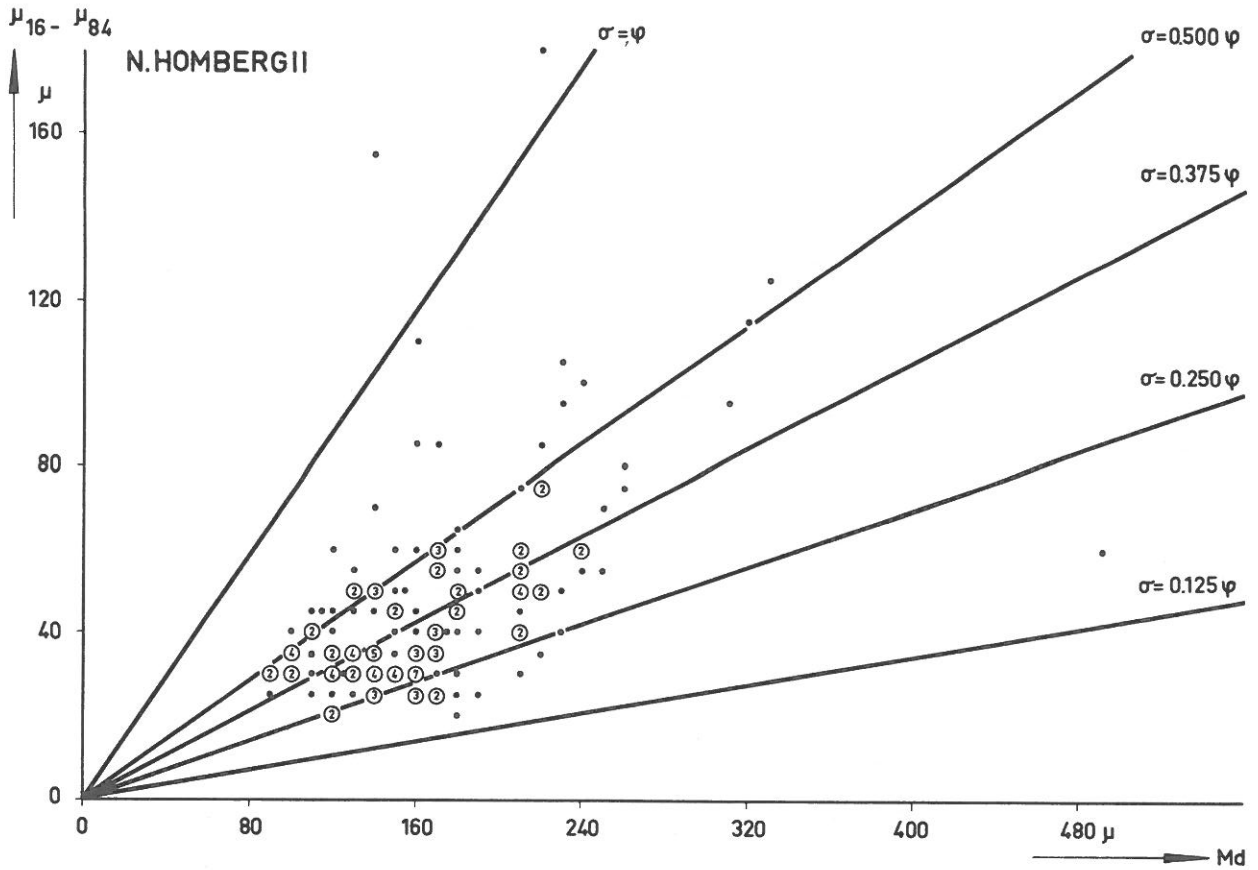

FIG. 11. — Rate of sorting of the sediments inhabited by *Nephtys hombergii*. Horizontal axis : median grain-size of the samples; vertical axis : sorting-coefficient in μ. Some lines connecting points with the same sorting-coefficient, expressed in φ-units, have been drawn.

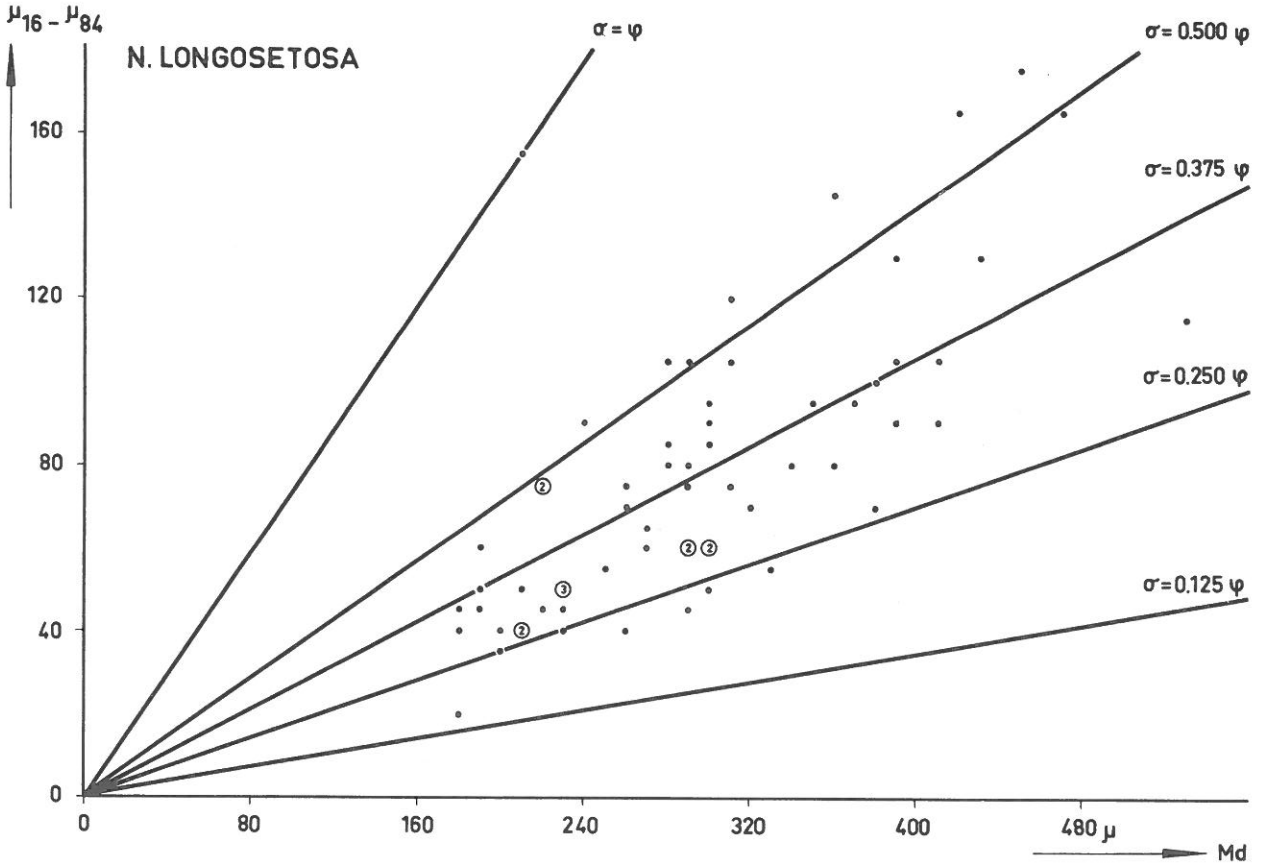

FIG. 12. — Rate of sorting of the sediments inhabited by *Nephtys longosetosa*. Horizontal axis : median grain-size of the samples; vertical axis : sorting-coefficient in μ. Some lines connecting points with the same sorting-coefficient, expressed in φ-units, have been drawn.

Nephtys in the Delta area is determined only by the nature of the sediment.

The data at our disposal permit a differentiation into three niches. *N. hombergii* lives in muddy sands, intertidally as well as subtidally. *N. caeca* lives only subtidally in somewhat coarser sediments than *N. hombergii*. *N. cirrosa* and *N. longosetosa* live together in clean sands, both intertidally and subtidally.

Although we did not find a separate niche for each species, this does not mean that they do not exist. I did not investigate the depth distribution within the substrate, for instance, nor did I study the food taken by these species. Moreover, it was shown by CROIN MICHIELSEN (1966) that two species of shrews probably differ only with respect to their distribution in winter, one of the species living mainly hypogeal in that period, and the other epigeal. Thus, eventual ecological differences may be very slight. Consequently, the fact that a differentiation into three niches was found with the rather crude methods applied, is an excellent result.

On the other hand, it is possible that this differentiation represents the maximum, because *N. cirrosa* and *N. longosetosa* exclude each other geographically to a large degree; these two species may indeed live within one and the same niche. This would of course imply the occurence of competition.

ACKNOWLEDGEMENTS

This study could not have been done without the help of many persons to whom I am greatly indebted. Messrs. P. de KOEIJER, W.J.L. ROBËR, C. de ROOIJ, A.J.J. SANDEE, and L. de WOLF helped with the field work and sorting of the samples. Mrs. C.H. BORGHOUTS-BIERSTEKER, Dr. C. den HARTOG, and Mr. W.J.M. VADER put material at my disposal collected during their investigations. Mr. J. NIEUWENHUIZE collected a large share of the grain-size data and calculated all the necessary grain-size parameters. Mr. J. VAN DER ENDE prepared the figures. Dr. K. FAUCHALD kindly checked some of my identifications of nephtyids. Mrs. I. SEEGER-WOLF improved the translation of the manuscript.

SUMMARY

Four species of *Nephtys* occur in the estuarine region of the rivers Rhine, Meuse, and Scheldt. These are *N. caeca, N. cirrosa, N. hombergii,* and *N. longosetosa.*

The results of the present study show that these species inhabit at least three separate ecological niches. *N. caeca* lives subtidally in muddy

sands; *N. hombergii* lives both intertidally and subtidally in even muddier sands. Differences in the rate of sorting of these sediments could not be demonstrated. *N. cirrosa* and *N. longosetosa* live together intertidally as well as subtidally in clean sands showing no differences in the range of the median grain-size or the rate of sorting.

Differences were also lacking in the reactions of the species to low salinities. Differences in depth distribution could be ascribed to the distribution of the sediments.

Although it is possible that not all the relevant ecological differences have been found, the fact that *N. cirrosa* and *N. longosetosa* have different geographical distributions which are almost mutually exclusive, must be given due weight, because it seems also possible that these two species inhabit the same ecological niche.

REFERENCES

BODDEKE, R., 1963. De invloed van de strenge winter 1962-1963 op de garnalenstand. *Viss. Nieuws,* **16** : 126-128.

BRAFIELD, A.E., 1964. The oxygen content of interstitial water in sandy shores. *J. Anim. Ecol.,* **33** : 97-116.

BRAFIELD, A.E., 1965. Quelques facteurs affectant la teneur en oxygène des eaux interstitielles littorales. *Vie Milieu,* **16** (2 A) : 889-897.

CALLAME, B., 1963. Le milieu interstitiel dans les sédiments sableux intercotidaux. *Bull. Inst. océanogr. Monaco,* **60** (1271) : 1-32.

CROIN MICHIELSEN, N., 1966. Intraspecific and interspecific competition in the shrews *Sorex araneus* L. and *Sorex minutus* L. *Archs néerl. Zool.,* **17** : 73-174.

CLARK, R.B. & E.C. HADERLIE, 1960. The distribution of *Nephtys cirrosa* and *Nephtys hombergii* on the south-western coasts of England and Wales. *J. Anim. Ecol.,* **29** : 117-147.

DAVIS, D.S., 1967. The marine fauna of the Blackwater Estuary and adjacent waters, Essex. *Essex Nat.,* **32** : 1-61.

FAUCHALD, K., 1963. Nephtyidae (Polychaeta) from Norwegian waters. *Sarsia,* **13** : 1-32.

FAUVEL, P., 1923. Polychètes errantes. Faune de France 5. 486 pp.

FRIEDRICH, H,. 1938. Polychaeta. Tierwelt Nord- und Ostsee 6 b. 200 pp.

HAMOND, R., 1966. The Polychaeta of the coast of Norfolk. *Cah. Biol. mar.,* **7** : 383-436.

HARTOG, C. DEN, 1963. The amphipods of the deltaic area of the rivers Rhine, Meuse, and Scheldt, in relation to the hydrography of the area. I. Introduction and hydrography. *Neth. Jnl Sea Res.,* **2** : 29-39.

HARDIN, G., 1960. The competitive exclusion principle. *Science,* **131** : 1292-1297.

INMAN, D.L., 1952. Measures for describing the size distribution of sediments. *J. Sed. Petrol.,* **22** : 125-145.

JOHNSON, R.G., 1965. Temperature variation in the infaunal environment of a sand flat. *Limnol. Oceanogr.*, **10** : 114-120.

JOHNSON, R.G., 1967. Salinity of interstitial water in a sandy beach. *Limnol. Oceanogr.*, **12** : 1-7.

JONES, J.D., 1955. Observations on the respiratory physiology and on the haemoglobin of the polychaete genus *Nephthys*, with special reference to *N. hombergii*. *J. exp. Biol.*, **32** : 110-125.

McINTYRE, A.D. & A. ELEFTHERIOU, 1968. The bottom fauna of a flatfish nursery ground. *J. mar. biol. Ass. U.K.*, **48** : 113-142.

PEELEN, R., 1967. Isohalines in the Delta area of the rivers Rhine, Meuse, and Scheldt. *Neth. Jnl Sea Res.*, **3** : 576-596.

POSTMA, H., 1957. Size frequency distribution of sands in the Dutch Wadden Sea. *Archs néerl. Zool.*, **12** : 319-349.

REID, D.M., 1932. Salinity interchange between salt water in sand and overflowing fresh water at low tide, II. *J. mar. biol. Ass. U.K.*, **18** : 299-306.

RULLIER, F., 1959. Étude bionomique de l'Aber de Roscoff. *Trav. Stn biol. Roscoff* (N.S.), **10** : 1-350.

SANDERS, H.L., P.C. MANGELSDORF & G.R. HAMPSON, 1965. Salinity and faunal distribution in the Pocasset River, Massachusetts. *Limnol. Oceanogr.*, **10**, suppl. : R216-R229.

SMITH, R.I., 1956. The ecology of the Tamar estuary. VII. Observations on the interstitial salinity of intertidal muds in the estuarine habitat of *Nereis diversicolor*. *J. mar. biol. Ass. U.K.*, **35** : 81-104.

SOUTHWARD, E.C., 1956. On some Polychaeta of the Isle of Man. *Ann. Mag. nat. Hist.*, (12) **9** : 257-279.

WESTHEIDE, W., 1966. Zur Polychaetenfauna des Eulitorals der Nordseeinsel Sylt. *Helgoländer wiss. Meeresunters.*, **13** : 203-209.

DISCUSSION
following the paper by W. J. WOLFF

VADER. — During the winters of 1961-1962, and 1962-1963, intertidal populations of *N. hombergii* in the Dutch Waddensea, disappeared completely during periods of frost, and dead specimens were found regularly. However, the populations returned in the course of the summer and autumn, probably by vertical migration from deeper waters. Did you notice the same in the Delta-area ?

WOLFF. — I was only able to study the intertidal populations of *N. hombergii* during some fairly mild winters. In these the majority of the population remained alive, but some losses were noticed in the higher part of the intertidal zone.

VADER. — Did you investigate the diet of the different species ? Even assuming that all are predators, differences in prey-animals diminishing interspecific competition, may exist.

WOLFF. — I did not investigate the food of the animals, but I noticed a few times that *N. hombergii* had taken other species of polychaetes, e.g. *Pygospio elegans* and *Scoloplos armiger*. Although it is possible that there are differences in the diet, it is my impression that these are only slight, because all species behave more or less omnivorous. However, this should be the subject of a closer investigation.

GEORGE. — Did you find that you were readily able to distinguish morphologically between the species investigated or was there an overlap in morphological characters ?

WOLFF. — After some training I was able to distinguish very well between specimens larger than about 2-3 cm. Smaller specimens may often also be identified, especially juveniles of *N. hombergii*. I did not notice any overlap in the morphological characters.